organs) the ants did not respond aggressively.

Not only were the behaviors of the attendant ants changed but also dopamine levels in their brains, which increased significantly in ants that attended caterpillars with functioning nectary organs. Other biogenic amines (serotonin, octopamine and tyramine) were not affected. Exactly how the secretions from the nectary organs could elicit such changes in an important neuromodulator and neurotransmitter remains unknown. The quantity of secretions from the nectary organs is very small, making a complete chemical characterization difficult. In addition, the researchers only measured four biogenic amines, but other changes in the brains of attendant ants might be taking place. Hopefully, future work such as whole brain metabolomics or RNA-seq experiments on individual brains will provide further insights.

But the importance of this paper is not just for the details it provides on the proximate mechanisms of behavioral manipulation [11]. The importance is also that apparently mutualistic caterpillars manipulate ant behavior at all. It is well known that parasites can adaptively manipulate the behavior of their hosts. This is the concept of the extended phenotype [12], where changes in host behavior benefit parasite fitness. In the study by Hojo *et al.* [2], it seems that attending bodyguard ants are less likely to wander from their charge and more likely to be aggressive, which should benefit the caterpillar. This 'mutualism' thus has all the hallmarks of adaptive manipulation of host behavior by a parasite!

It would appear that caterpillars enforce the cooperation they require. This is likely to be due to the fact that the ant colony may not need its caterpillar 'sugar tap' as much as the sugar tap needs its fierce bodyguards. As other sources of sugar present themselves, the danger for the caterpillar is that the ants shift away from their protective role, leaving the caterpillar vulnerable to predation. And so, perhaps by way of an insurance mechanism, the hungry caterpillar has evolved to keep their ant bodyguards on a short leash using manipulative drugs. This study will hopefully encourage different researchers to examine other apparent manipulations for signs of similar manipulative behaviors.

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Plant Intracellular Transport: Tracing Functions of the Retrograde Kinesin

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Adding to its varied repertoire of functions in cell morphogenesis and cell division, a molecular motor protein of the kinesin-14 class has recently been implicated in rapid retrograde transport along cellular tracks in moss.

Like traffic in general, cellular trafficking also relies on dedicated tracks and vehicles that facilitate the transport of cargo. In all eukaryotes, transport tracks are made of the cytoskeleton — polar microtubules and actin filaments. Aided by versatile molecular motors, the list of cellular mechanisms requiring the cytoskeleton is nearly infinite, and includes diverse functions in cell division, cell polarization and growth as well as in subcellular transport. In most eukaryotes,

cargo transport along these cellular tracks is assisted by three motor protein families — the microtubule-dependent kinesins, the dyneins and the actin-dependent myosins. However, the microtubule minus-end directed dyneins were lost from flowering plants and are absent from most clades of the lower plants [1], raising the question of exactly how plant cells accomplish minus-end directed, retrograde microtubule-dependent transport. Members of the minus-end directed kinesin-14 class motor proteins might substitute for dynein to achieve retrograde transport functions; yet, until recently, processive motility was only confirmed for kinesin-14 in yeast, but was reported neither for animal nor plant kinesin-14.

In a new study, published recently in *Nature Plants*, [2], Jönsson and co-workers now show that a member of the kinesin-14 class motor proteins in the moss *Physcomitrella patens* performs retrograde transport towards the minus-end of microtubules. In moss, the kinesin-14 class encompasses six subdivisions, kin-14I to kin-14VI, and based on subcellular localization they were assigned mitotic and non-mitotic functions [3]. The authors used advanced imaging of *in vitro* microtubule gliding assays to visualize the directional displacement of polarity-marked microtubules by purified kinesin-14 motors attached to glass cover slips. Four of the six representative kinesin-14s tested displayed microtubule minus-end directed motility as dimers [2]. To analyze the motors' processivity *in vitro,* single-molecule motility assays were performed, where labeled microtubules were bound to a cover slip and dilute kinesin-14 preparations were added [2]. Processive motors stay attached to the microtubule, even when walking over long distances, while non-processive motors detach immediately after each step. In these experiments, none of the investigated kin-14 motor-dimers demonstrated processive movement [2].

Nevertheless, one motor domain, kin-14VIb, displayed particularly fast microtubule gliding velocity and, therefore, the full-length kin14VIb (FL) protein was examined for processivity. Despite the majority of dimeric kin-14VIb (FL) remaining non-processive, some brighter, mobile particles revealed the presence of a small number of processively moving kin-14VIb. This processive movement originated from the clustering of two or more kin-14VIb dimers, akin to the processive movement of an artificial kin-14VIb tetramer [2]. In support of the notion that the processive behavior of kin-14VIb depended on multiple motor dimers, clustering of kin-14VIb on liposomes enabled liposome transport along microtubules [2].

Finally, fluorescently labeled, endogenous kin-14VIb punctae moved processively along microtubules in moss protonemal cells, and comparison of signal intensities with protein complexes of known fluorophore numbers suggested that the mobile kin-14VIb punctae indeed contained more than one dimer [2]. The authors conclude that the clustering of a few non-processive kin-14VIb dimers collectively enables the processive microtubule minus-end directed movement in the moss. Although the potential cargos are still elusive, it seems that the search for the retrograde microtubule-dependent motor has come to a closure in the moss.

However, this finding leads to the question of which functions kin-14VIb motor might have in other plants. Indeed, the homologue of kin-14VIb in flowering plants, kinesin-like calmodulin-binding protein (KCBP), has been extensively studied *in vitro* and *in vivo* [4–9]. KCBP binding to calcium-calmodulin inhibits the motor's microtubule binding ability [10–12] and likely this is also the case for moss kin-14VIb. *Arabidopsis* KCBP is a minus-end directed motor *in vitro* [10], and in cotton KCBP displays punctate localization along microtubules [7] in agreement with the findings for moss kin-14VIb [2]. Further indicative of a possible transport function of KCBP is the formation of abnormal leaf hairs in the *Arabidopsis KCBP* mutant *zwichel* [5]. Yet processive motility, as shown for moss kin-14VIb, has not been reported for flowering plant KCBP so far. In addition to the non-mitotic function, the flowering plant KCBPs serve diverse roles in cell division — KCBPs associate with mitotic microtubule arrays and inhibition of KCBP function during mitosis delays cytokinesis [4,7–9], features that have not been reported for moss kin-14VIb [2,3].

Recently, adding a new twist to KCBP's function in flowering plants, KCBP was attributed to the plant specific mode of division plane positioning [8]. Plant cells are immobilized within tissues due to their confinement by cell walls; therefore, spatio-temporal control over cell divisions is crucial for plant development. Plant cells do not divide by constriction, but instead form a new partitioning wall, the cell plate, in the cell center during cytokinesis. KCBP was recently implicated in the guidance mechanism that attracts the cell plate to its final destination [8], which is pre-selected prior to mitosis by a transient band of microtubules, the plant-specific preprophase band [13]. The preprophase band disassembles, but leaves behind a set of 'landmark' proteins, collectively referred to as the cortical division site, that is required to preserve the positional information of the preprophase band throughout mitosis [13,14]. The recently revealed presence of KCBP at the cortical division site paves the way for speculation whether KCBP-mediated forces might contribute to the unique cell plate guidance mechanisms [8].

Thus, the kin-14VIb/KCBP microtubule-minus end-directed motors emerge as versatile motor proteins that replace dynein as a retrograde transporter in the moss, and likely in the entire plant lineage, pending proof of processive movement. It should be noted here that rapid subcellular transport has been attributed to the actin–myosin cytoskeleton [15]. However, plant-specific mitotic KCBP functions might have evolved concurrent with the transition from simple to complex plant architecture in the context of cell wall-imposed positional confinement. Consistent with their plant-specific functions, the kin-14VIb/KCBPs are found only in plants and in green algae, underpinning their evolution in the green lineage [16,17]; their motor domain, however, originates before the divergence of plants and animals [17].

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